CHEMICAL MEDIATION OF COEVOLUTION: PHYLOGENETIC EVIDENCE FOR APIACEAE AND ASSOCIATES[1]

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ABSTRACT

The chemical diversity of the Apiaceae has made the family of particular significance in discussions of plant/insect interactions for close to a century. As forbs with distinctive chemistry and a specialized insect fauna, species in the Apiaceae and their associated herbivores represent an ideal system for examining competing hypotheses accounting for hostplant acquisition patterns. Comparisons of the phylogenetic history of colonization of Apiaceae across a number of taxa reveal that host shifts to the family originate in only a narrow range of taxa; chemical similarities among those taxa, rather than geographic proximity or phylogenetic relationships, are the most plausible basis for the observed host shifts. Similar ecologies among species in this narrow range of taxa, including similar herbivore faunas, may well account for similarities in overall chemical profiles. The patterns documented here are consistent with reciprocal coevolutionary interactions between herbivorous insects and their hostplants.

Key words: Agonopterix, Apiaceae, coevolution, *Depressaria, Euleia,* furanocoumarin, *Greya,* insect-plant interaction, *Oreina, Papaipema, Papilio.*

The family Apiaceae contains over 3000 species worldwide; these can be found in a wide range of habitats, including deserts, marshes, basaltic bluffs, forests, subalpine tundra, woodlands, and wasteplaces (Berenbaum, 1990). Morphologically, the Apiaceae are a fairly conservative family, one of the few so-called "natural plant families" of Theophrastus of Eresus (the "father of botany"). Theophrastus recognized the taxonomic significance of the "naked seeds" that characterize some members of the group (the pair of one-seeded mericarps that constitute a schizocarp), as well as the distinctive umbelliform inflorescence. These plants were classified as *Narthekodes,* from the Greek *Narthex,* meaning "plant." In Latin, the group acquired the name *Ferulacea;* the term "Umbelliferae" did not appear until the late sixteenth century, with Daleschamps's 1586 *Historia generalis plantarum* as an example (Constance, 1971). To the Apiaceae goes the distinction of being the first plant family to be monographed, when Robert Morison published his *Plantarum umbelliferarum distributio nova* in 1672 (Hedge, 1973; Downie et al., 1998).

In striking contrast with their morphological conservatism, the Apiaceae display considerable diversity in chemistry. The earliest manifestations of these chemical differences appear in the myriad ways in which apiaceous plants have been used historically by cultures all over the world. Everywhere they grow, they have been utilized throughout the ages by people for all manner of purposes. In his *Greek Herbal,* Dioscorides listed close to 50 different Apiaceae among his useful plants, most of which were classified as "herbs." The aromatic nature of many apiaceous plants, attributable to essential oils in glands on seeds and elsewhere, makes them well suited for this function. Dill (*Anethum graveolens* L.), coriander (*Coriandrum sativum* L.), fennel (*Foeniculum vulgare* Mill.), cumin (*Cuminum cyminum* L.), and anise (*Pimpinella anisum* L.) have filled this role more or less continuously since that time. Petrified caraway seeds (*Carum carvi* L.) were excavated from prehistoric Lake Dwellings in Switzerland (Rohde, 1922). As well, many members with tuberous roots or analogous structures have found use as staple foods—carrots (*Daucus carota* L.), parsnip (*Pastinaca sativa* L.), and celery (*Apium graveolens* L.) among them. Although, as French (1971: 387) pointed out, "no known civilization has been based on the cultivation of parsnips or carrots," in North America,

the Nez Perce used the swollen roots of *Perideridia* and *Lomatium* species as a staple food source.

In large part due to their diverse chemistries, apiaceous plants have found ubiquitous use for a panoply of disorders and diseases, including, among others, gastrointestinal disturbances, respiratory diseases, urogenital problems (including syphilis), and skin problems (wounds, bites, stings, boils, rashes, and warts). A few have found use as aphrodisiacs. According to Dioscorides, "Parsley—especially Bastard or Wild Parsley—provokes venery and bodily lust & erection of the parts" (Rohde, 1922). Carrots were used to treat jaundice in Europe, most likely because of their orange color, in an apparent application of the doctrine of signatures (French, 1971). Rycharde Bankes's 1525 *Herball*, possibly the first herbal printed in Britain, devoted quite a bit of text to apiaceous plants. Caraway was recommended "to destroy wycked wynds and y coughe; it is good for y frenesy & for bytynge of venemous beestes; for scabbes & teters." He also claimed the oil "restoreth heere as it is fallen awaye." As for celery, according to Bankes, "The virtue of this Herbe is thus: it wyll make a man to pysse and open y stoppynge of y lyver." The seed "ground well with Seed of Rue/ pepper & salt/ then mixt with Wyne & drunke/ was goode for the colde & wycked humoures in y stomake/lyver or longes." With respect to chervil (*Anthriscus cerefolium* (L.) Hoffmann), "the vertue of this herbe is thus: it shall make a man to pysse well . . . if it be dronken with Wyne it delyuereth a man of ache in the raynes [kidneys] & letteth out and unbyndeth y wycked wyndes." John Gerard was perhaps the most well known of English herbalists—*The Herball or generall historie of plantes* was published in 1597. According to Gerard, "Caruwaies consume winde; are delightful to the stomacke and taste and provoke urine." In 1649, Nicholas Culpepper produced his *Physicall Directory (an Astrologo-Phisical Discourse of the Vulgar Herbs of this Nation: Containing a Compleat Method of Physick, whereby a man may preserve his both in Health; or Cure himself, being Sick, for three pence Charge, with such things only as grow in England, they being most fit for English Bodies* (1661 edition) (Arber, 1938). In this work, angelica (*Angelica archangelica* L.) was recommended as a tonic, stimulant, carminative, expectorant, and diaphoretic, as well as a remedy for warding off devils and witches.

Chemical potency underlies the historical use of Apiaceae for not-so-therapeutic purposes as well. In ancient Greece, one of the plants used for the execution of criminals, *Conium maculatum* L. (poison hemlock), was used for dispatching Socrates for corrupting the morals of Athenian youth (Fairbairn, 1971). In imperial Rome, plant poisoning was an important factor in determining patterns of primogeniture and succession. The practice of plant poisoning probably reached its peak in medieval Europe, and in the courts of Italy and France apiaceous species were routinely included in the poisoner's arsenal. The twelfth century herbal of Apuleius, for example, specifically makes note of the poisonous properties of water dropwort, *Oenanthe crocata* L. (which was employed as a fish poison when it was not being used for more insidious purposes).

Chemical Diversity Documented

The ethnobotanical importance of the Apiaceae, specifically of Apiaceae subfamily Apioideae, is a reflection of the remarkable chemical diversity within the family; these plants are distinctive in the diversity, abundance, and uniqueness of their chemistry. Throughout the nineteenth and twentieth centuries, as the scientific study of analytical chemistry and then phytochemistry grew more sophisticated, an impressive inventory was documented. Apiaceae, for example, are well endowed with essential oil constituents. Although they share monoterpenes with a large number of taxa, they are distinctive in producing certain essential oil constituents and non-volatile biosynthetically related compounds. The characteristic terpenoids of Apiaceae include esters of monoterpene aldehydes, daucan-type sesquiterpenes, ligustilide-type compounds, and guaianolide and germacranolide sesquiterpene lactones (Hegnauer, 1971).

Also present as essential oil constituents are phenylpropanoid derivatives. There are at least five different groups of phenylpropenes, based on patterns of hydroxylation of the benzene ring (Harborne, 1971). One widespread representative of 3,4,5-trihydroxy-substituted phenylpropenes is myristicin, containing a methylenedioxyphenyl (MDP) ring; this compound is reported to occur in 14 genera within the family. Isoeugenol epoxide esters are found in Apiaceae, but they are extremely rare outside the family. Also unusual among plants are the 2-methylchromones that characterize Apiaceae.

Other phenylpropanoid derivatives include the coumarins; the Apiaceae produce these compounds in abundance and diversity rivaled by few other families (Berenbaum, 1991). Among the distinctive coumarin derivatives are both linear and angular furanocoumarins; pyranocoumarins are also frequently found. Although hydroxycoumarins are

widespread among plants, occurring in over 30 families, the presence of isopentenyl-substituted coumarins in abundance further distinguishes the Apiaceae from other families.

Polyacetylenes are yet another hallmark of the family, occurring in all three subfamilies (Bohlmann, 1971). Whereas C-17 polyacetylenes (such as falcarinol) are most frequently encountered, C-13 and C-15 polyacetylenes are also known from a variety of taxa.

Alkaloid production is extremely limited within the Apiaceae, being more or less restricted to the genus *Conium*. The structural type represented within this genus is relatively unusual. Coniine and related piperidine alkaloids are narrowly distributed throughout the plant kingdom and are best known from this genus. The deadly action of poison hemlock is attributable to the presence of these alkaloids, which function as potent neurotoxins to vertebrates (Fairbairn, 1971).

Finally, even storage compounds are chemically distinctive within the Apiaceae (Hegnauer, 1971). Seeds generally contain large quantities of fatty oils; virtually universal in occurrence throughout the family is the fatty acid petroselinic acid, rarely found elsewhere. As for carbohydrates, the raffinose isomer umbelliferose is a family character.

ECOLOGICAL SIGNIFICANCE OF APIACEAE CHEMISTRY

The distinctive nature of the chemistry of Apiaceae typified a pattern that had been revealed by the last quarter of the nineteenth century after inspection of a broad range of plants. Perhaps most distinctive was the fact that there were certain types of chemicals possessed to some degree by all plants—chlorophyll, for one, used as a photosynthetic pigment, or the amino acids that make up plant proteins. Others were exceedingly idiosyncratic in their distribution—restricted to only a single family, genus, or even species of plant, and varying with season, climate, soil type, and even age of the individual plant. It was reasoned that such compounds were unlikely to be essential to the day-to-day physiological needs of a plant and thus they were called secondary compounds. The Apiaceae proved to be an excellent source of these secondary compounds.

If these compounds play no role in primary physiological processes, the question then arose as to what their function really is in the plant. By the mid-nineteenth century, a hypothesis was put forward. In a study of the relationships between snails and plants, Stahl (1888—quoted in Fraenkel, 1959: 1466) remarked:

"We have long been accustomed to comprehend many manifestations of the morphology [of plants] . . . as being due to the relations between plants and animals, and nobody, in our special case here, will doubt that the external mechanical means of protection of plants were acquired in their struggle. . . with the animal world . . . . In the same sense, the great differences in the nature of chemical products [Excrete] and consequently of metabolic processes, are brought nearer to our understanding, if we regard these compounds as means of protection, acquired in the struggle with the animal world. Thus, the animal world which surrounds the plants deeply influenced not only their morphology, but also their chemistry."

Secondary compounds, then, were suggested to play an important ecological function to the plant—by mediating its interactions with other organisms. The Apiaceae have been a key focus for testing this hypothesis over the years. Brues (1920: 322), writing on associations between plants and insects, remarked that the family is infrequently colonized by insects due to its diverse and conspicuous chemistry (e.g., "We may readily see that the generally strong-scented Labiatae and Umbelliferae and the milky Euphorbiaceae might require great adaptation on the part of larvae eating them"). It did not escape his notice that the insects associated with these plants are highly specialized. Dethier (1941) traced patterns of chemical similarity among hosts of *Papilio* swallowtails, including Apiaceae, and suggested that chemical similarities among plants, particularly in essential oil constituents, may facilitate colonization of novel hostplants.

Fraenkel (1959) resurrected Stahl's notion of chemical mediation of ecological interactions and bolstered it with the accumulated empirical evidence of the intervening seven decades that ecological interactions were in fact the raison d'être of plant secondary compounds. The Apiaceae were one of six families of plants and their associates provided as examples of how chemical similarities underlie patterns of hostplant use by specialized herbivores. Moreover, he provided an evolutionary mechanism to account for the idiosyncratic distribution of plant secondary chemicals—what he called reciprocal adaptive evolution.

Five years later, Ehrlich and Raven (1964) dubbed this reciprocal process coevolution and proposed a multi-step scenario to account for diversification of secondary metabolism—

1. by mutation or recombination, plants acquire a novel chemical compound; by chance, this com-

pound reduces the suitability of the plant as food for herbivores;

2. protected from herbivory, the plant can enter a new adaptive zone and diversification can take place;

3. by mutation or recombination, a phytophagous insect acquires the means to detoxify or otherwise tolerate the erstwhile toxin and thus can utilize the previously protected plant;

4. this insect then enters a new adaptive zone and can undergo evolutionary diversification;

5. the erstwhile toxin can become a host recognition cue or attractant for its adapted herbivores.

Again, Apiaceae and their insect associates provided fuel for the argument. In particular, these authors remarked on the ability of species in the genus *Papilio* to feed freely on Rutaceae and Apiaceae, two chemically similar families; yet despite the close taxonomic relationship between Apiaceae and Araliaceae, no papilionid butterflies were known at the time to feed on species in the latter family.

With their multistep scenario, Ehrlich and Raven suggested that coevolution between insects and plants was responsible at least in part for the tremendous diversification of these two groups and hence for the diversity observed in most terrestrial ecosystems. Thus, this coevolutionary process, subsequently labeled the "escape and radiate" model (Thompson, 1999), accounts not only for the biochemical diversity of angiosperm plants and herbivorous insects, but also for the tremendous diversification of plant secondary compounds.

Ehrlich and Raven's (1964) paper inspired decades of both theoretical and empirical work designed to document all or part of the evolutionary scenario. Berenbaum (1983) combined literature and original data to apply the stepwise scenario to furanocoumarins, a group of apiaceous secondary chemicals. Furanocoumarins are typical secondary compounds in that they are idiosyncratically distributed among plants. They have been reported from only a handful of angiosperm families, and they are ubiquitous and diverse in only two families—Rutaceae and Apiaceae. Within the Apiaceae, they are common only in the subfamily Apioideae. There are two classes of furanocoumarins—linear, with the furan ring attached in line with the coumarin nucleus, and angular, with the furan ring at the 7,8 position and hence at an angle. The citrus and carrot families have been long known to physicians as having phytophotodermatitic properties. Casual contact with the aboveground parts results in the eruption of painful blisters, followed in severe cases by permanent scarring and

elevated pigmentation of the skin. The agents responsible for these conditions are the furanocoumarins (Berenbaum, 1991). They are relatively unusual among plant compounds in that, in the presence of ultraviolet light, they are able to cross-link strands of DNA and hence prevent transcription. Thus, they are toxic to a wide range of organisms, including bacteria, fungi, and some viruses; plants containing furanocoumarins cause problems to livestock including ducks, geese, cattle, horses, and pigs; and they are, of course, toxic to insects.

All known furanocoumarins are thought to derive from a single biosynthetic precursor, umbelliferone (7-hydroxycoumarin). Umbelliferone and related hydroxycoumarins, occurring in approximately three dozen plant families, are far more widespread among plant families than are the derivative furanocoumarins. Among the furanocoumarins the two principal structural classes derive from the activity of two different location-specific prenylating enzymes: linear, with the prenyl group ring attached at the 6 position, and angular, with the prenyl group attached at the 8 position. Linear furanocoumarins, known from about a dozen plant families, are more widely distributed in turn than are the angular furanocoumarins, which are restricted to approximately three plant families. When tested against a generalist insect, linear furanocoumarins are appreciably more toxic than are hydroxycoumarins, and, when tested against an adapted specialist, angular furanocoumarins are more toxic than are linear furanocoumarins. This progressive increase in toxicity, corresponding to biosynthetic advancement, is consistent with the Ehrlich and Raven scenario. Moreover, as Ehrlich and Raven predicted, plant taxa with more advanced coumarins are more species-rich than are taxa with less advanced coumarins, and insect taxa feeding on plants with higher coumarins are more species-rich than are taxa feeding on plants with simple coumarins (Table 1). This increase in diversity was interpreted as evidence of the existence of Ehrlich and Raven's "adaptive zones." Similarly, lepidopteran groups associated with hostplants with advanced coumarins (such as furanocoumarins) are more species-rich than close relatives that are associated with plants containing only simple coumarins (Table 1), again suggesting entry into a new adaptive zone with subsequent diversification.

The suggestion that the evolution of biochemical innovations in plants and insects initiates adaptive radiation led Mitter and Brooks (1984) to predict that coevolution between plants and animals should lead to parallel cladogenesis—essentially, that these alternating periods of diversification in con-

Table 1. Putative adaptive radiations associated with biochemical novelties in Apiaceae-insect associations (LFC = linear furanocoumarin, AFC = angular furanocoumarin, HC = hydroxycoumarin). (Berenbaum, 1983.)

A. Chemical diversity in genera within Apiaceae

Coumarin chemistry	Avg. no. spp./genus
Without furanocoumarins or with dihydroxyfuranocoumarins only	12.1 ± 3.6
With linear furanocoumarins only	17.4 ± 5.8
With linear and angular furanocoumarins	67.3 ± 16.8

B. Species diversity within the genus *Papilio* according to hostplant chemistry

Papilio section	Hostplant chemistry	No. spp.
Section II	LFC, AFC, HC	139
Section IV	LFC, HC	34
Section V	HC	18
Section I	HC	9
Section III	HC	8

C. Species diversity within the Depressariinae according to hostplant chemistry

Depressariine genus	Hostplant chemistry	No. spp.
Depressaria	LFC, AFC, HC	100
Agonopterix	LFC, AFC, HC	125
Exaeretia	HC	38
Apachea	LFC, HC	1
Bibarrambla	HC	1
Nites	NC	5

cert will be reflected in the evolutionary record as phylogenies with identical topologies. This suggestion stimulated a wave of effort among systematists to compare cladograms of herbivorous insects and their associated hostplants. There have been some striking examples of congruent cladogenesis, e.g., *Tetraopes* and their milkweed hosts (Farrell & Mitter, 1998), but the majority of tests have failed to document such patterns. At the same time, studies of other groups have revealed patterns that are entirely inconsistent with parallel cladogenesis and are more consistent with models of sequential evolution, whereby insects colonize plants long after taxonomic and chemical diversity have evolved, rather than coevolution. Menken (1996) examined relationships among nine western European *Yponomeuta* moth species and determined that, within this species-group, four hostplant families representing three orders are utilized. Even for species groups utilizing a single hostplant family, phylogenetic relationships among insect herbivores do not necessarily reflect tribal relationships among hostplants (Funk et al., 1995).

The fact that patterns other than parallel cladogenesis have been demonstrated, with perhaps greater frequency, has been interpreted by some (Jermy, 1993; Schoonhoven et al., 1998) as a justification for rejecting coevolution as a mechanism for species interaction. Cited in support of this rejection is literature suggesting that insects rarely act as selective agents on their hostplants—a necessary prerequisite to reciprocal selection. Many still maintain this position (Schoonhoven et al., 1998), despite abundant evidence that under certain circumstances insect herbivores can indeed exert selection on their hostplants (Marquis, 1992). Another factor leading to skepticism about coevolution is the temporal incongruence of taxa; in many cases, it is clear that plant hosts diversified long before insect colonization took place (Futuyma, 1983; Funk et al., 1995). Thompson (1999) argued, however, that the Ehrlich and Raven (1964) scenario does not in fact predict parallel cladogenesis at all; rather, the phylogenetic pattern that is generated by stepwise reciprocal evolution is one of alternating "starburst" episodes of diversification. Thus, the infrequency of congruent cladogenesis does not in itself lead to a rejection of coevolution.

A more reasonable view of interaction between plants and insect herbivores is that coevolution is not a universal phenomenon characterizing all forms of interactions between herbivorous insects and their hostplants, but that it successfully describes some forms of interactions at particular taxonomic levels under certain ecological circumstances. Indeed, given the staggering abundance of plant-feeding insects and the plants they consume, the expectation of a single model of any sort seems unrealistic at best. Moreover, the intense focus on insect and plant systematics and phylogeny has led many investigators to overlook the putative chemical mediators of the process. Tests of chemical facilitation of hostplant shifts and subsequent diversification are few and far between.

Janz and Nylin (1998) conducted a study that sheds some light on the nature of sequential colonization. Appropriately, these authors reexamined the groups that had originally inspired Ehrlich and Raven (1964) to propose their coevolutionary scenario. In this study, a butterfly phylogeny was assembled from a broad array of studies and was compared with a plant phylogeny derived from molecular analyses (Chase et al., 1993). From this study, the authors concluded that host shifts do tend to occur between closely related plants, with

Table 2. Specialist insects in North America exclusively or almost exclusively associated with Apiaceae (Berenbaum, 1990).

Genus		Number of specialists/ number in genus	Feeding habits[a]
Homoptera			
Aphididae	*Aphis*	5/153	PS
	Cavariella	4/11	PS
	Hyadaphis	1/2	PS
Hemiptera			
Miridae	*Orthops*	1/11	PS
Diptera			
Psilidae	*Psila*	1/1	RM
Agromyzidae	*Phytomyza*	14/	LM
Tephritidae	*Euleia*	1/2	LM
Coleoptera			
Curculionidae	*Apion* (*Fallapion*)	4/10 (125 total)	SM
	Smicronyx	2/69	SM
	Listronotus	1/28	RM
Lepidoptera			
Prodoxidae	*Greya*	3/15	SM
Oecophoridae	*Agonopterix*	7/34	LF
	Depressaria	18/21	LF
Epermeniidae	*Epermenia*	3/3	SM, LM
Noctuidae	*Papaipema*	2/22	SB
Papilionidae	*Papilio*	11/26	LF

[a] PS = phloem sucker, RM = root miner, LM = leaf miner, SM = seed miner, LF = leaf and flower chewer, SB = stem borer.

colonization of more distantly related plants more common in tree-feeding taxa. They suggested that a possible mechanism underlying the facility with which tree-feeding taxa colonize new hosts is the reduced degree of chemical differentiation among trees, relative to forbs. Thus, for tree-feeding species, the expectation of coevolutionary interactions—and hence parallel cladogenesis—should be low; correspondingly, for forb-feeding species, the expectation should be higher.

ACQUISITION OF APIACEAE HOSTPLANTS—
PHYLOGENY OR CHEMISTRY?

As forbs with a specialized insect fauna and diverse chemistry, the Apiaceae and their associated herbivores (Table 2) represent an ideal system for examining competing hypotheses accounting for hostplant acquisition. The principal insect associates in North America are in the order Lepidoptera, notably in the family Papilionidae; within the genus *Papilio*, a group of approximately six species within the *machaon* complex are associated with Apiaceae. Also within the Lepidoptera is the family Oecophoridae (in part; now subfamily Depressari-

inae in Elachistidae); two genera, *Depressaria* and *Agonopterix*, are noteworthy in the extent to which species utilize apiaceous hostplants. Within the genus *Papaipema* (Noctuidae), Apiaceae-feeding is also well documented, as it is for a handful of microlepidopteran species in the Prodoxidae and Epermeniidae.

In Diptera, there are representatives of two families associated with Apiaceae; within the family Agromyzidae, several species of *Phytomyza* are specialists, forming distinctive linear leaf mines in the foliage of their hosts. Also mining the leaves of apiaceous hostplants are species of Tephritidae in the genus *Euleia*.

Within other orders, feeding on Apiaceae is infrequently encountered (Burki & Nentwig, 1997). Among Coleoptera, specialization on Apiaceae is found in at least two families: Curculionidae (*Apion* and, in Europe, *Liophloeus*) and Chrysomelidae (in Europe, *Oreina*). There are relatively few hemimetabolous insects specialized on Apiaceae—among them are *Aphis/Cavariella/Anuraphis* (Aphididae) and, in Europe, *Eupteryx aurata* (Cicadellidae) in Homoptera, and *Orthops* in Hemiptera. In part due

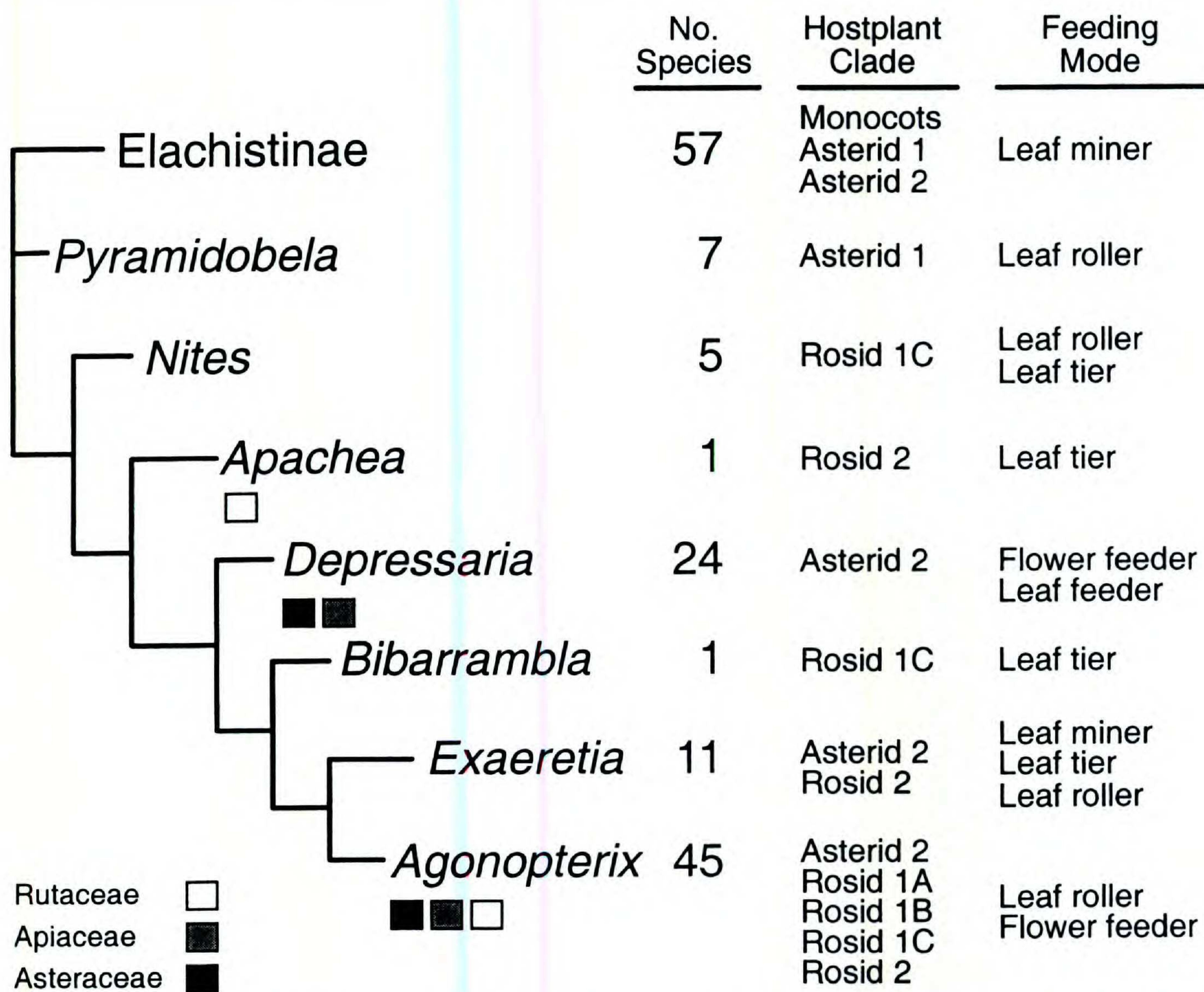|	No. Species	Hostplant Clade	Feeding Mode
Elachistinae	57	Monocots Asterid 1 Asterid 2	Leaf miner
Pyramidobela	7	Asterid 1	Leaf roller
Nites	5	Rosid 1C	Leaf roller Leaf tier
Apachea	1	Rosid 2	Leaf tier
Depressaria	24	Asterid 2	Flower feeder Leaf feeder
Bibarrambla	1	Rosid 1C	Leaf tier
Exaeretia	11	Asterid 2 Rosid 2	Leaf miner Leaf tier Leaf roller
Agonopterix	45	Asterid 2 Rosid 1A Rosid 1B Rosid 1C Rosid 2	Leaf roller Flower feeder

Rutaceae ☐
Apiaceae ▨
Asteraceae ■

Figure 1. Phylogenetic relationships and hostplant associations in depressariine Elachistidae (modified from Berenbaum & Passoa, 1999; plant clades as in Chase et al., 1993).

to the economic importance of the Apiaceae, and in part due to general recognition of the importance of the family as a paradigm for the study of coevolution, a remarkable number of phylogenetic studies have been conducted to date on the herbivores associated with the family.

DEPRESSARIINES

Berenbaum and Passoa (1999) recently completed an analysis of phylogenetic relationships among the depressariine Oecophoridae (= Elachistidae) (Fig. 1). The Depressariinae can be defined as a monophyletic insect group based on the tubular mesothoracic spiracle, a character first noted by Nakamura (1981). In the Depressariinae, *Agonopterix* and *Depressaria*, the only two Apiaceae-feeding Nearctic depressariines, are both monophyletic. Although *Depressaria* is defined by a homoplasious apomorphy, at least the two major North American Apiaceae-feeding species groups within the genus (*pastinacella* and *douglasella*) are defined by au-

tapomorphies in their male genitalia and larval pinacula (S. Passoa & M. Berenbaum, unpublished data). A phylogeny for *Agonopterix* is not presently available.

The existence of monophyletic groups is important because within the context of coevolution adaptive radiations occur due to the acquisition of key innovations associated with overcoming plant defenses (Ehrlich & Raven, 1964). Farrell et al. (1992) suggested that sister-group comparisons could be used to determine whether an adaptive radiation has taken place; because sister groups are equal in age, a significantly greater number of species in one branch could be construed as evidence of evolutionary success. *Agonopterix*, with 42 species, is more diverse than its sister group *Exaeretia*, with 10 species, at least in North America (Hodges et al., 1983). On a generic level, *Depressaria*, with 24 species, is less diverse than its sister group, composed of *Bibarrambla* (1 species), *Exaeretia* (10 species), and *Agonopterix* (43 species). In contrast,
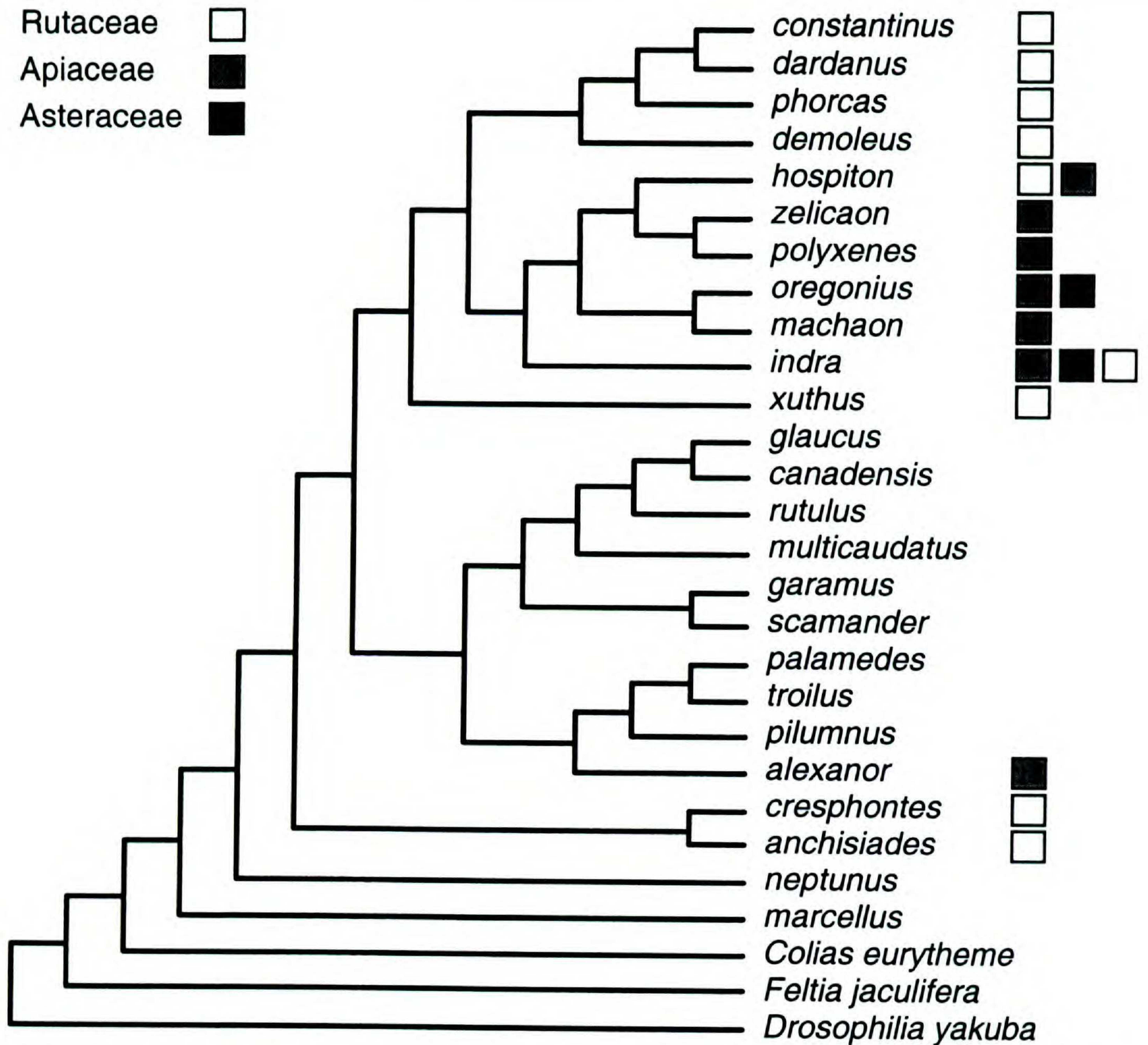
Figure 2. Phylogenetic relationships and hostplant associations in *Papilio* (Lepidoptera: Papilionidae) (modified from Caterino & Sperling, 1999).

within the genus *Depressaria*, half of the species (12 of 24) belong to the *douglasella* group, and no other group has more than five species (Hodges, 1974). Because *Agonopterix* and *Depressaria* are not sister groups, the Apiaceae must have been independently colonized at least twice by Depressariinae.

The results of this work on the North American fauna confirm that Rutaceae-feeding in the genus *Apachea* is ancestral to umbellifer-feeding in *Depressaria* and *Agonopterix*. The same pattern is suggested in European Depressariinae from phenetic studies (Hannemann, 1953, 1958), but no cladistic analysis of either North American or European Depressariinae existed at the time.

PAPILIO

Caterino and Sperling (1999) sequenced 2.3 kb of DNA from the mitochondrial cytochrome oxidase

I and II genes for a number of species in the genus *Papilio*. They identified five major lineages—*machaon-phorcas-demoleus-xuthus*, *cresphontes-anchisiades*, *glaucus-garamas-scamander*, *troilus*, and *alexanor*. According to this analysis (Fig. 2), Apiaceae-feeding arose at least two times, in each case from Rutaceae-feeding ancestors (*alexanor*, *machaon* complex, *demoleus* group (*demodocus*)). The ancestral relationship of Rutaceae-feeders to Apiaceae/Asteraceae feeders in both the tribe Papilionini and the subfamily Depressariinae argues for a historical progression rather than simply opportunistic colonization of chemically related plants.

PAPAIPEMA

Papaipema species in the family Noctuidae are stem-borers, mostly of herbaceous plants. Most are oligophagous and a number feed exclusively on
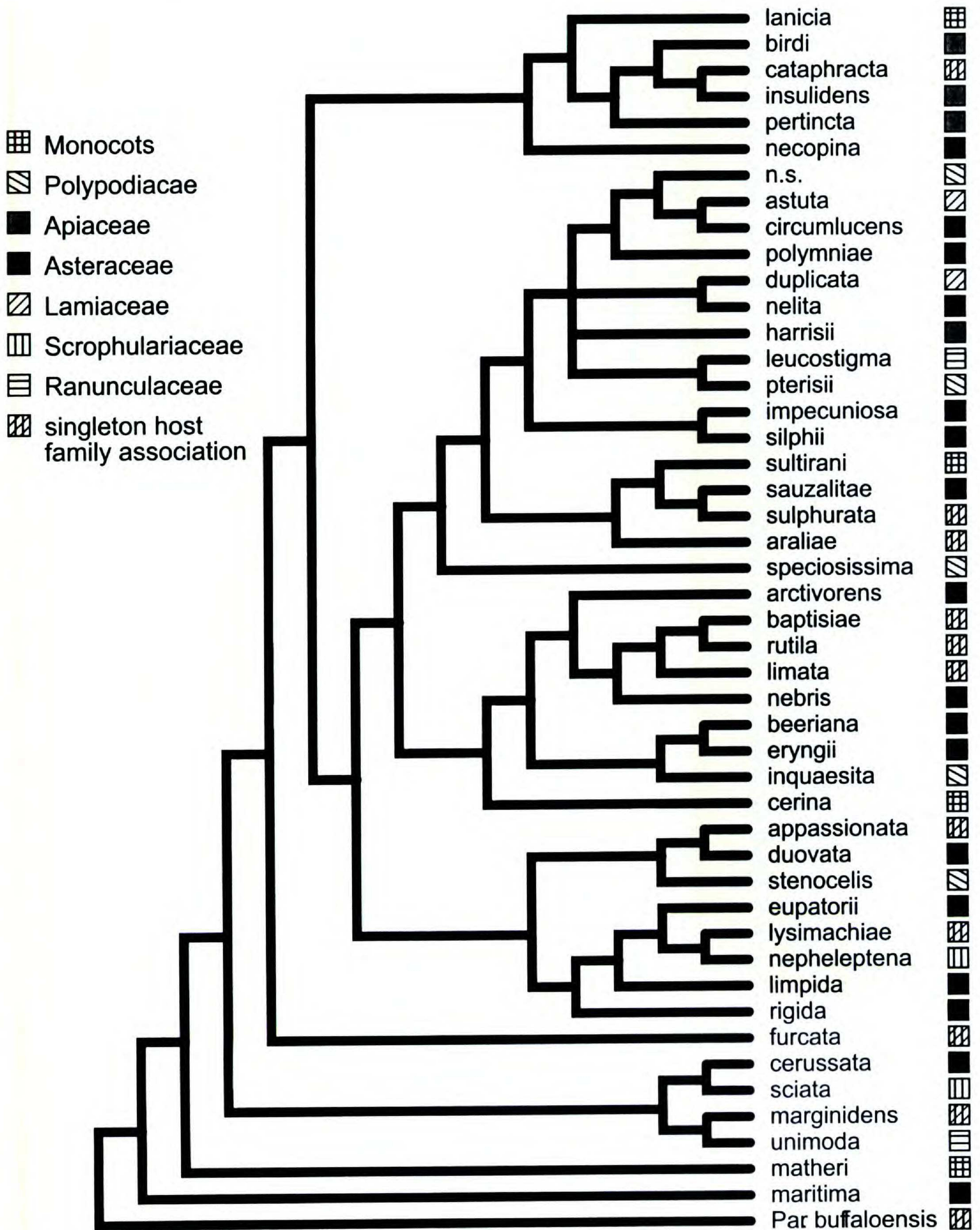
Figure 3. Phylogenetic relationships and hostplant associations in *Papaipema* (Lepidoptera: Noctuidae) (modified from Goldstein, 1999, and pers. comm.).

Apiaceae. Goldstein (1999) recently completed an examination of patterns of colonization of Apiaceae by species in the genus *Papaipema* (Fig. 3). Phylogenetic analysis suggests three independent origins of Apiaceae-feeding within *Papaipema*; no instances of Apiaceae-feeding can be found in apameine noctuids outside *Papaipema*. The Apiaceae feeders consist of *P. eryngii*, which appears as sister to an Asteraceae-feeding species; *P. harrisii*, which falls directly within an Asteraceae-feed-

Saxifragaceae ⊠
Apiaceae ■

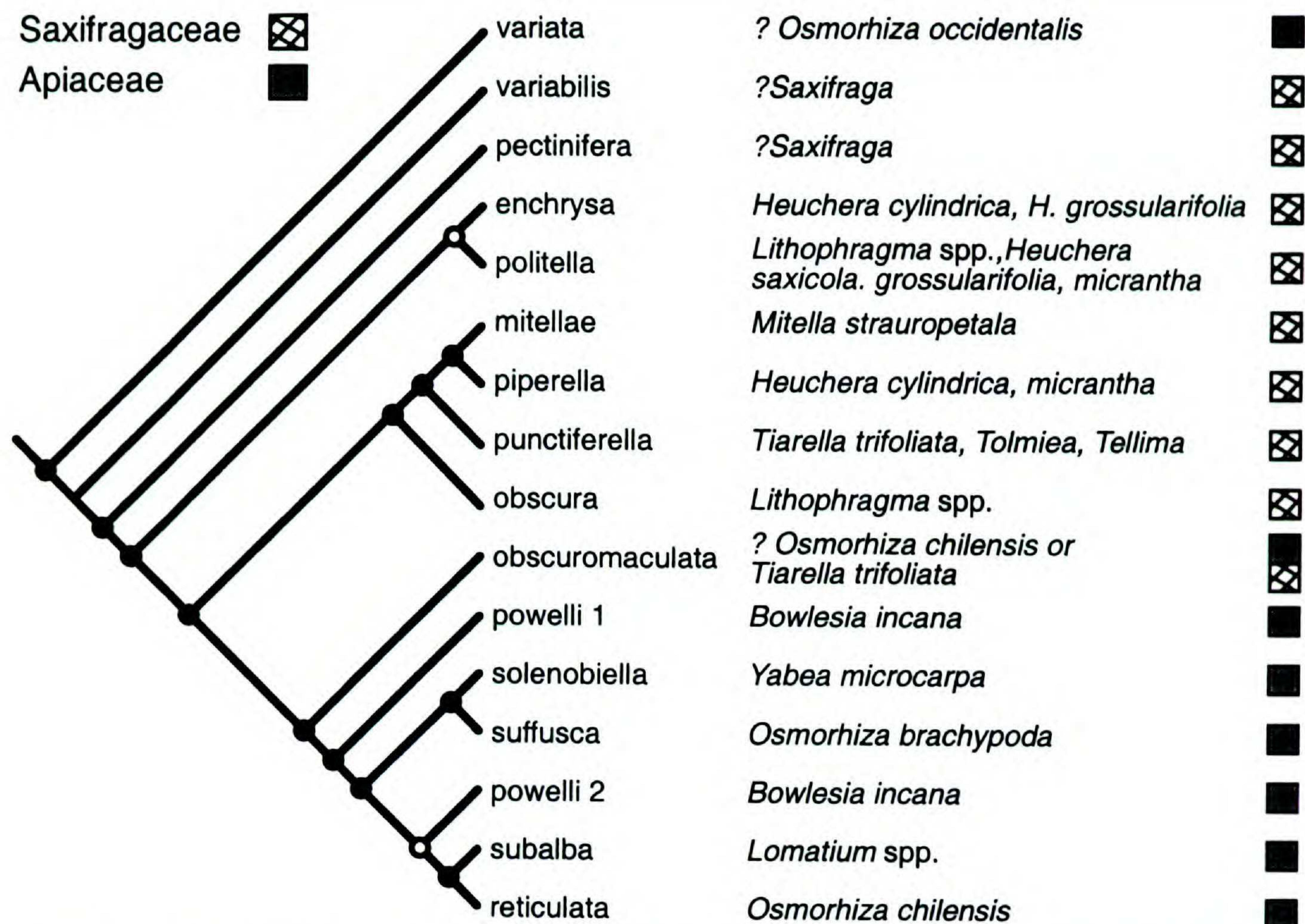| Species	Hostplant	
variata	*? Osmorhiza occidentalis*	■
variabilis	*?Saxifraga*	⊠
pectinifera	*?Saxifraga*	⊠
enchrysa	*Heuchera cylindrica, H. grossularifolia*	⊠
politella	*Lithophragma* spp.,*Heuchera saxicola. grossularifolia, micrantha*	⊠
mitellae	*Mitella strauropetala*	⊠
piperella	*Heuchera cylindrica, micrantha*	⊠
punctiferella	*Tiarella trifoliata, Tolmiea, Tellima*	⊠
obscura	*Lithophragma* spp.	⊠
obscuromaculata	*? Osmorhiza chilensis or Tiarella trifoliata*	■ ⊠
powelli 1	*Bowlesia incana*	■
solenobiella	*Yabea microcarpa*	■
suffusca	*Osmorhiza brachypoda*	■
powelli 2	*Bowlesia incana*	■
subalba	*Lomatium* spp.	■
reticulata	*Osmorhiza chilensis*	■

Figure 4.   Phylogenetic relationships and hostplant associations in *Greya* (Lepidoptera: Prodoxidae Incurvarioidea) (modified from Brown et al., 1994).

ing clade; and the *P. birdi* group, which appears as paraphyletic on the tree, but which, depending on optimization, may also have arisen from an aster-feeding clade. It is noteworthy that the *birdi* group appears as paraphyletic to the generalist species *P. cataphracta*, which is recorded from many asteraceous species but only one apiaceous species, with that being a dubious record.

GREYA

Brown et al. (1994) found that Apiaceae-feeding prodoxid moths form a phylogenetic unit. Apiaceae-feeders in this group are monophyletic; sister taxa are most likely associated with Saxifragaceae (Fig. 4). This host shift is very likely attributable to the fact that species in both host families occupy similar habitats in close geographical proximity; few if any chemical similarities are known to exist between these two families.

EULEIA

Although the majority of Tephritidae (4000 species in 500 genera) are fruit or flower feeders, species in the genus *Euleia* are unusual in that they are leaf miners (as are all members of the subtribe

Tripetina). Han and McPheron (1997) conducted an analysis of tephritid phylogeny using sequence data from the mitochondrial 16S ribosomal DNA (925 base pairs). Within the monophyletic Trypetini, Apiaceae-feeding is a derived trait and represents a shift from Asteraceae-feeding ancestors (Fig. 5).

PHYTOMYZA

At least 15 species of *Phytomyza* (Diptera: Agromyzidae) are leaf miners of apiaceous plants. If there is a cladistic analysis of phylogeny, it is not readily available. However, it is interesting to note that at least four species (*P. albiceps, P. chrysanthemi, P. nigra,* and *P. obscurella*) are reported on both apiaceous and asteraceous hostplants.

OREINA

Dobler et al. (1996) examined hostplant switches in the chrysomelid genus *Oreina*, a Palearctic genus with approximately 24 species, most of which are alpine in distribution. Hostplant range includes *Oreina gloriosa* on a single species *Peucedanum ostruthium* (L.) W. Koch, to *O. bifrons* on two hosts in different tribes (*Peucedanum* and *Chaerophyl-*
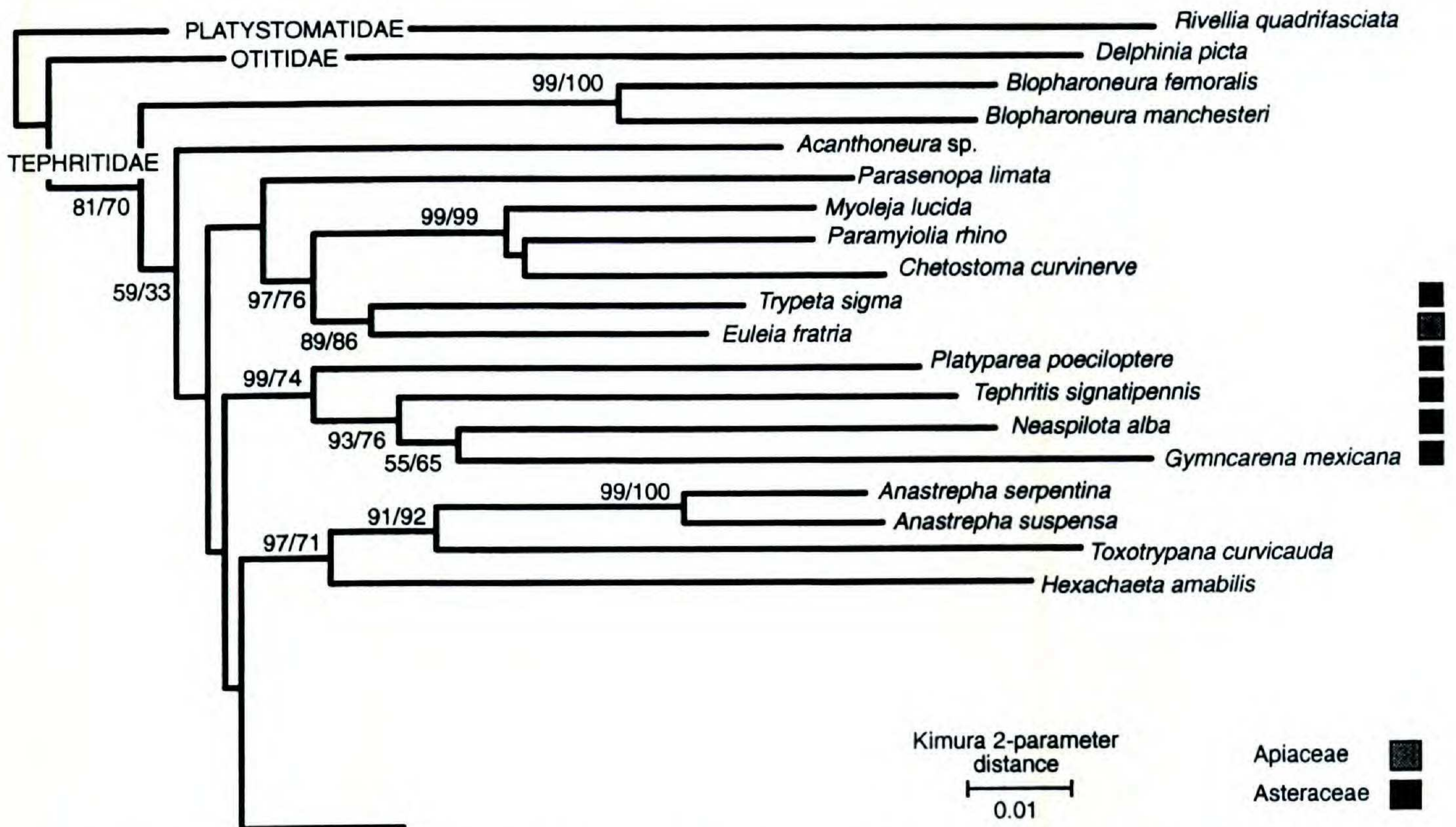
Figure 5. Phylogenetic relationships and hostplant associations in *Euleia* (Diptera: Tephritidae) (modified from Han & McPheron, 1997).

lum), to species on Apiaceae in three different tribes. The majority of species feed on Asteraceae in two tribes, Senecioneae and Cardueae. One species, *Oreina frigida*, accepts both Asteraceae and Apiaceae. These authors conducted a cladistic analysis of 18 allozyme loci (Fig. 6). Dobler et al. (1996) generated two most parsimonious trees, which demonstrated that the ancestral host for *Oreina* was most likely Asteraceae; Apiaceae occur in the diet of one oligophagous species and its occurrence in a derived clade represents an independent switch. The two asteraceous tribes utilized by these insects are phylogenetically "distant."

COMPARISONS AMONG TAXA

An examination of the phylogenetic history of colonization of Apiaceae across taxa reveals some inescapable patterns. Host shifts to the Apiaceae originate in only a narrow range of plant taxa. In four cases (twice within the depressariine elachistids and twice within the genus *Papilio*), Rutaceae-feeding is ancestral to Apiaceae-feeding, and in five cases (three in *Papaipema*, one in *Oreina*, and one in *Euleia*), Asteraceae-feeding is ancestral to Apiaceae-feeding. There are several possible explanations as to why this should be. Phylogenetic relationship can almost certainly be ruled out, however. The most likely sister family to the Apiaceae is the Araliaceae (Downie et al., 1998), and there is virtually no evidence of Araliaceae-feeding

in any relative (distant or close) of an Apiaceae-feeder. By the same token, the sister family of Asteraceae, the hosts for immediate ancestors of a number of Apiaceae-feeders, is regarded by many (Bremer & Gustafsson, 1997) to be the Campanulaceae, again, a family absolutely absent from the host records of relatives of Apiaceae-feeders.

Another common explanation for host shifts is geographic or ecological proximity. Such an explanation is plausible for Asteraceae-Apiaceae shifts; both families are primarily temperate herbaceous and occupy similar habitats. There are many other families that share early successional habitats with the hostplants of these insect groups, including species of Lamiaceae, Brassicaceae, Polygonaceae, and Fabaceae, to name but a few, but host shifts from these groups to Apiaceae are non-existent. Geographic or ecological proximity is even less satisfying as an explanation for shifts to Apiaceae from Rutaceae, given that the Rutaceae consists primarily of trees and shrubs that are mostly tropical in origin.

Patterns of host shifts in Apiaceae associates parallel patterns of hostplant colonization among the butterflies (Janz & Nylin, 1998: plant classifications that follow according to this source). As do butterflies, a high proportion of depressariine oecophorid species use Rosidae as hostplants (all *Nites*, *Apachea*, and *Bibarrambla*, and 11 of 42 *Agonopterix*). If, in fact, the Amphisbatinae are an-
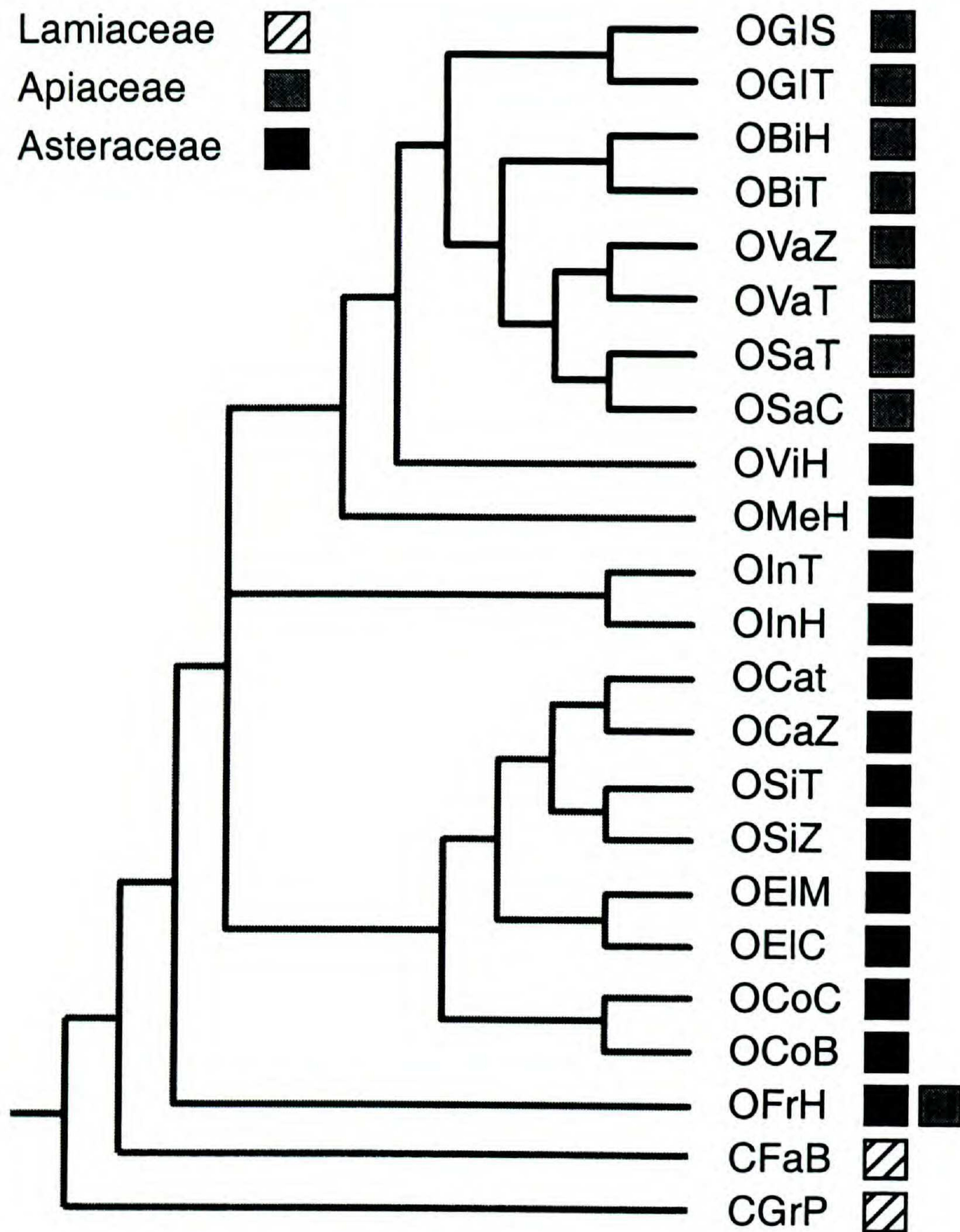
Figure 6. Phylogenetic relationships and hostplant associations in *Oreina* (Coleoptera: Chrysomelidae) (modified from Dobler et al., 1996). Species names include *O. bifrons* (O BiH, O BiT), *O. cacaliae* (O CaT, O CaZ), *O. coerulea* (O CoB, O CoC), *O. elongata* (O ElC), *O. frigida* (O FrH), *O. gloriosa* (O. GlS, O GlT), *O. intricata* (O InH, O InT), *O. melanocephala* (O MeH), *O. speciosa* (O SaC, O SaT), *O. speciossissima* (O SiT, O SiZ), *O. variabilis* (O VaT, O VaZ), *O. virgulata* (O ViH).

cestral to the Depressariinae-Ethmiinae clade (Passoa, 1995), then the Rosidae may be the ancestral hostplants; contemporary Amphisbatinae utilize representatives of Rosid 1A (Salicaceae), Rosid 1B (Ulmaceae), and Rosid 1C (Betulaceae, Fagaceae, Juglandaceae) clades. As is true for butterflies, genera associated with trees predominate; there is no obvious trend toward specialization on forbs at this level, and there is no evidence of a tendency for advanced insect taxa to feed on advanced plant taxa. Association with plants in the asterid 2 clade appears to have led to rapid speciation. The two most species-rich genera in the group, *Depressaria* and *Agonopterix*, are dominated by species that

feed on Apiaceae and Asteraceae; all of the *Depressaria* species with known feeding habits are found on these plant families, and 19 of 42 *Agonopterix* species feed predominantly or exclusively on these plants.

Chemistry provides an extremely attractive organizing principle to account for patterns of colonization and diversification in virtually all taxa associated with Apiaceae. The distinctive groups of secondary chemicals shared by Asteraceae and Apiaceae include cyclitols, isoeugenol epoxides, germacranolides, guaianolides, and eudesmanolide sesquiterpene lactones, 2-methyl chromones, petroselinic acid, triterpene sapogenins, polyacetylenes

Table 3. Phytochemical characteristics of Apiaceae, plants utilized by Apiaceae-feeders, and sister taxa to plant groups utilized by Apiaceae-feeders (phytochemical data from Hegnauer, 1971).

Phytochemical	Api-aceae	Arali-aceae	Ruta-ceae	As-tera-ceae	Cam-panu-laceae
Essential oils	x	x	x	x	
Furanocoumarins	x		x		
Pyranocoumarins	x		x		
Isopentenyl coumarins	x		x	x	
Polyacetylenes	x	x		x	x
Triterpenic saponins	x	x		x	x
2-methyl chromones	x		x	x	
Guaianolides	x			x	
Germacranolides	x			x	
Petroselinic acid	x				
Tannins lacking	x	x		x	x
Lignans	x	x	x	x	

(although in Asteraceae these tend to be cyclic, with aromatic or heteroaromatic terminal groups), and coumarins. These families also have the absence of certain chemicals in common; both lack ellagitannins, proanthocyanidins, and iridoids. The chemical resemblances between these families are all the more striking considering the generally lower level of chemical resemblance between sister taxa. The Asteraceae have more chemistry in common with the Apiaceae than with the Campanulaceae, widely regarded as the sister group; by the same token, although Apiaceae and its sister group Araliaceae share many chemicals, there are more different types of secondary compounds in common between Apiaceae and Asteraceae (Table 3).

Thus, the question remains—why do distantly related plant taxa have more similar chemistries than closely related taxa? Convergence in morphological traits in plants arises as a result of common ecologies—desert-dwelling plants have reduced leaf area to conserve water, and bee-pollinated plants have zygomorphic aromatic blue flowers to attract their mutualists. Similar ecologies, including similar herbivore faunas, could account for similarities in overall chemical profile. These patterns are actually suggestive of reciprocity—it is difficult otherwise to provide a scenario to account for such remarkable convergences (other than common ancestry, which, according to systematists, is not the likely explanation). Chemical innovation can lead to adaptive radiation—and it can also lead to colonization by preadapted species. In a study aimed at determining the basis for host shifts by species of flea beetle in the genus *Blepharida*, Becerra and

Venable (1999) found that geographic similarity and phylogenetic relatedness could not account as well for the patterns observed as could hostplant chemistry; for specialists within the genus, plant chemical similarity appears to be the best explanation for shifts within this group.

Similar selection pressures can increase the probability of parallel evolution. The key, then, is the preadaptation of the insects to co-occurring groups of chemicals. Considerable evidence exists that co-occurring chemicals can interact in additive and synergistic ways (Berenbaum, 1985; Berenbaum & Zangerl, 1996); these combinations of chemicals thus can exert selection pressures quite unlike those exerted by component chemicals in isolation. There is also experimental evidence that insects adapt to combinations of chemicals in distinctive ways. Methylenedioxyphenyl compounds in Apiaceae (e.g., myristicin) and Asteraceae (e.g., sesamin), for example, are associated with potentiation of furanocoumarins; these MDP compounds act as inhibitors of cytochrome P450 monooxygenases, the enzymes largely responsible for furanocoumarin detoxification in herbivorous insects. Specialists on Apiaceae show greater resistance to the P450-inhibiting effects of these compounds, and concomitantly greater tolerance of co-occurring furanocoumarins, than do insects that normally do not encounter these compounds together (Neal & Wu, 1994; Zumwalt & Neal, 1993). Thus, combinations of toxins and synergists present a different toxicological challenge to insects, and counteradaptation presents a different resistance challenge to plants, in which a narrower range of chemistries may be available to overcome resistance. Similar faunas can thus be expected to select for plants with similar kinds of chemistry.

Colonization of a new hostplant by an insect is possible only if parents can locate the hosts and immature feeding stages are equipped metabolically to deal with the hosts. It is thus not altogether surprising that insects sharing certain chemically distinct hostplants colonize new hostplants in similar fashion, and in doing so they jointly act to affect evolution in those hostplants. In nature, then, as in human culture, it appears inexorably that there really are a limited number of ways to eat an umbellifer—a limited number of evolutionary approaches—due to the unique nature of its chemistry.

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